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A Chromosome-Specific Estimate of Transmission of Heterozygosity by 2*n* Gametes in Potato

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Polyploid plants are formed when numerically unreduced (2*n*) gametes participate in fertilization. Based on cytological and genetic analyses, modes of 2*n* gamete formation have been determined for a number of plant species. Gametes formed by a first-division restitution (FDR) mechanism contain nonsister chromatids near the centromere, whereas those formed by second-division restitution (SDR) contain sister chromatids. These mechanisms differ in the proportion of heterozygous loci they transmit intact to offspring. This paper estimates the transmission of heterozygosity on an individual chromosome basis through pachytene analysis of chromosomes of haploids ($2n = 2x = 24$) of *Solanum tuberosum* Andigena Group ($2n = 4x = 48$), a South American cultivated potato. Transmission of heterozygosity by FDR and SDR 2*n* gametes was calculated for 6 different cytogenetic assumptions. FDR was more than twice as effective as SDR in transmission of heterozygosity under all 6 scenarios. Rates of transmission of heterozygosity were similar in each situation. Transmission of heterozygosity by FDR was also compared with transmission of heterozygosity by tetrasomic inheritance and found to be approximately 50% more effective.

Potato geneticists from 10 countries on 4 continents have reported heterosis for potato tuber yield in tetraploid progeny following 4*x*-by-2*x* crosses (Jansky and Peloquin 2006). The tetraploid ($2n = 4x = 48$) parents were potato (*Solanum tuberosum* L.) cultivars or advanced selections. Some diploid ($2n = 2x = 24$) parents were hybrids between *S. tuberosum* Phureja Group clones and Tuberosum Group haploids. Others were hybrids between Tuberosum Group haploids and wild diploid *Solanum* species. All diploid parents were homozygous for the recessive parallel spindles meiotic mutation (*ps*), which produces numerically unreduced (2*n*) gametes via a first-division restitution (FDR) mechanism. Researchers have also compared tuber yields of tetraploid families from 4*x*-by-2*x* (FDR), 4*x*-by-2*x* [second-division restitution (SDR)], and 4*x*-by-4*x* matings (Mok and Peloquin 1975). Nine tetraploid potato cultivars or advanced selections were crossed with each other and with 4 diploid FDR clones and 4 diploid SDR clones. The families from 4*x*-by-2*x* FDR crosses outyielded the 4*x*-by-2*x* SDR and 4*x*-by-4*x* families by about 50%. Because intra- and interlocus interactions contribute to high yield in potato, this significant increase in yield by 4*x*-by-2*x* FDR families has been interpreted as due to the increase in transmission of heterozygosity and epistasis by 2*n* FDR gametes (Mendiburu and Peloquin 1977).

Studies of the cytological basis of 2*n* gamete production have been carried out in a number of plant species (see reviews in Veilleux 1985; Bretagnolle and Thompson 1995; Ramanna and Jacobsen 2003). Although several mechanisms of 2*n* gamete production have been reported, most can be divided into 2 categories based on their genetic consequences. FDR mechanisms lead to 2*n* gametes that contain nonsister chromatids between the centromere and the first crossover. Consequently, all loci between the centromere and the first crossover that were heterozygous in the diploid parent will be heterozygous in the gametes. Half of those beyond the crossover will be heterozygous in the gametes. SDR mechanisms lead to 2*n* gametes that contain sister chromatids between the centromere and the first crossover. All loci between the centromere and the first crossover that were heterozygous in the diploid parent will be homozygous in these 2*n* gametes, whereas those beyond the crossover will be heterozygous.

Estimates of transmission of heterozygosity by FDR and SDR gametes on the basis of centromere location in potato indicate that FDR is twice as effective as SDR (Peloquin 1983; Hermsen 1984). A more precise estimation of transmission of heterozygosity requires additional cytological

details about individual chromosomes, such as relative length, amount of heterochromatin, and average number of chiasmata. Although these data are not available for most plant species, a detailed cytological analysis of potato chromosomes has been published including evaluations of relative chromosome length, euchromatin and heterochromatin content, centromere location, and observations of usually one chiasma per bivalent (Yeh et al. 1965). These data can be used to test the effects of various cytological models on the amount of heterozygosity transmitted through FDR and SDR mechanisms. This will determine whether generalizations about transmission of heterozygosity are reasonable approximations in the absence of cytological details.

Because tetraploid plants produce diploid gametes, they are also capable of transmitting heterozygosity through gametes. Segregation patterns in tetraploids depend on the location of the gene in question relative to the centromere (see Little 1945, 1958; Burnham 1962). At one extreme, absolute linkage to the centromere leads to chromosome segregation. At the other extreme, a crossover frequency of 100% between the gene and the centromere results in maximal equational separation. The frequency of double reduction (gametes carrying sister chromatids) is 0 for chromosome segregation and 1/6 for maximal equational separation segregation. A third scenario, chromatid segregation, is similar to maximal equational separation, with a frequency of double reduction equal to 1/7. In this model, it is assumed that alleles on chromatids segregate randomly due to an infinite number of crossovers between the centromere and the locus in question.

The objective of this study is to measure the transmission of heterozygosity in potato on an individual chromosome basis based on cytological data. Transmission of heterozygosity by 2*n* gametes under 6 different cytogenetic conditions is determined, and transmission of heterozygosity by FDR 2*n* gametes in diploids is compared with that of *n* gametes in tetraploids.

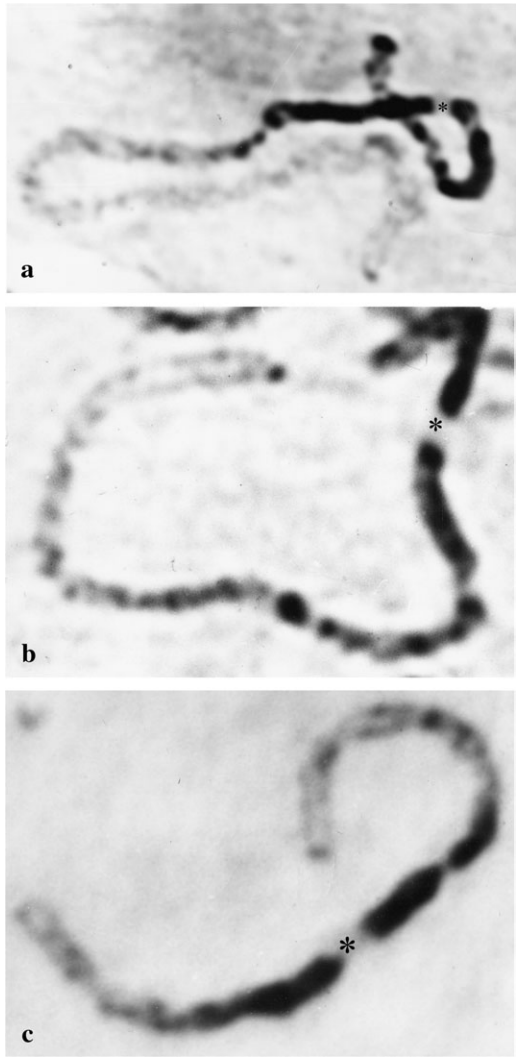

Figure 1. Representative pachytene chromosomes in potato: (a) chromosome I (3:1 arm ratio), (b) chromosome IV (5:1 arm ratio), and (c) chromosome XII (1:1 arm ratio). Centromeres are indicated by asterisks.

Materials and Methods

Measurements were made on pachytene chromosomes of haploids ($2n = 2x = 24$) of *S. tuberosum* Andigena Group ($2n = 4x = 48$) using images published by Yeh et al. (1965). Photographs of chromosomes were enlarged, and total length, arm ratio, and length of euchromatic regions were measured in arbitrary units. Final values were based on the mean of 2–3 photographs of each chromosome. The description of each chromosome includes centromere location and the presence of secondary constrictions, distinct chromomeres, and characteristic telochromomeres. It is recognized that the measurements are not precise because the appearance and length of the chromosomes varies during late pachytene, and uneven stretching during slide preparation adds to this variation. Furthermore, the distinction between heterochromatin and euchromatin regions is somewhat arbitrary.

Transmission of heterozygosity by FDR and SDR 2*n* gametes was calculated for 6 different sets of cytogenetic assumptions: 1) all 12 chromosomes are of equal length, with a single crossover in each chromosome; 2) all chromosomes are of equal length and double crossovers occur in chromosomes I, II, and V, whereas single crossovers occur in the remaining chromosomes; 3) chromosome lengths vary based on cytological data, and a single crossover occurs in each chromosome; 4) chromosome lengths vary based on cytological data with double crossovers in I, II, and V, and single crossovers in the remaining chromosomes; 5) the effective chromosome size is that of the euchromatic regions, and a single crossover occurs in each chromosome; and 6) the effective chromosome size is that of the euchromatic regions, and double crossovers occur in I, II, and V, whereas single crossovers occur in the remaining chromosomes. In each situation, the crossover event was assumed to occur midway between the centromere and the

Table 1. Length, arm ratio, percent euchromatin, and total amount of euchromatin for each of the 12 chromosomes of potato

Chromosome	Total[a]	Short[a]	Long[a]	Arm ratio	Percent euchromatin	Euchromatin total[b]
I	99.00	25.50	73.50	3:1	74.0	0.74
II	89.00	7.00	82.00	10:1	75.0	0.84
III	69.00	12.00	57.00	5:1	55.0	0.80
IV	61.80	10.25	51.50	5:1	46.0	0.74
V	62.00	28.50	33.50	1:1	46.0	0.74
VI	63.50	17.00	46.50	3:1	41.5	0.73
VII	57.00	15.00	42.00	3:1	45.0	0.79
VIII	47.50	16.00	31.50	2:1	38.0	0.80
IX	41.00	13.00	28.00	2:1	38.0	0.80
X	37.30	12.50	25.00	2:1	21.0	0.56
XI	46.00	20.50	19.50	1:1	29.0	0.72
XII	35.00	17.00	18.00	1:1	21.0	0.66

[a] Arbitrary units.

[b] Total length × percent euchromatin.

telomere. If one crossover occurred, then it happened on the longest chromosome arm. If 2 crossovers occurred, they were found on both arms unless the chromosomes were subtelocentric (chromosome II).

Transmission of heterozygosity by n gametes of the common tetraploid potato ($2n = 4x = 48$) was also calculated based on 3 different cytogenetic assumptions: 1) 2 alleles per locus and chromosome segregation, 2) 2 alleles per locus and 10% chromatid segregation, and 3) 2 alleles per locus and 50% chromatid segregation.

Results and Discussion

The characteristics of potato chromosomes are illustrated by 3 representative chromosomes in Figure 1. Chromosome I is one of the longest chromosomes and has a 3:1 arm ratio; chromosome IV is a medium-sized chromosome and has a 5:1 arm ratio; and chromosome XII, with a 1:1 arm ratio, is representative of the 5 smallest chromosomes. The total relative chromosome length at late pachytene, arm ratio, length of euchromatic regions, and transmission of heterozygosity by FDR and SDR of each of the 12 chromosomes are presented in Table 1. Chromosomes V, XI, and XII have a 1:1 arm ratio; chromosomes VIII, IX, and X have a 2:1 arm ratio; chromosomes I, VI, and VII have a 3:1 arm ratio; chromosomes III and IV have a 5:1 arm ratio; and chromosome II has a 10:1 arm ratio. The longest chromosome is almost 3 times the length of the shortest and the amount of euchromatin varies more than 3-fold among chromosomes. The fraction of euchromatin relative to total length varies from 0.56 in X to 0.84 in II. In most chromosomes, the amount of euchromatin is 70–80% of the total chromosome length.

The transmission of heterozygosity by each chromosome varies with centromere location (Table 2). Assuming a single crossover, chromosomes with median centromeres transmit 87.5% with FDR and 25% with SDR. Chromosome II is subtelocentric, with a 10:1 arm ratio and transmits 77.3% of its heterozygosity with FDR and 45.5% with SDR.

The total transmission of heterozygosity, assuming all chromosomes are equal in genetic content (length) and a single crossover occurs in each chromosome, is 82.7% with FDR and 34.7% with SDR. The results do not differ greatly from these values when calculated based on either chromosome length (80.6 and 36.7), length of euchromatin (81.0 and 36.0), or the occurrence of double crossovers in 3 of the 12 bivalents (Table 3). Three ring bivalents were regularly found at metaphase I in these plant materials (Yeh et al. 1964) indicating the occurrence of double crossovers in these chromosomes. Two- and four-strand double crossovers have no effect on transmission of heterozygosity if both crossovers occur within one arm of the chromosome, whereas three-strand double crossovers reduce heterozygosity by 50% for distal genes. Consequently, double crossovers have minimal effect in reducing the transmission of heterozygosity. If, however, a crossover occurs in each arm of a metacentric chromosome, it significantly affects the heterozygosity transmitted by that chromosome. A metacentric chromosome with a crossover in one arm transmits 87.5% of its heterozygosity with FDR and 25% with SDR. In contrast, when there is a crossover in each arm, the transmission of heterozygosity with FDR is

Table 2. Percent transmission of heterozygosity from individual chromosomes based on arm ratio and length, assuming one crossover per chromosome

Chromosome	Arm ratio	FDR	SDR
I	3:1	81.3	37.5
II	10:1	77.3	45.5
III	5:1	79.2	41.7
IV	5:1	79.2	41.7
V	1:1	87.5	25.0
VI	3:1	81.3	37.5
VII	3:1	81.3	37.5
VIII	2:1	83.3	33.3
IX	2:1	83.3	33.3
X	2:1	83.3	33.3
XI	1:1	87.5	25.0
XII	1:1	87.5	25.0

Table 3. Percent transmission of heterozygosity by FDR and SDR 2*n* gametes and FDR/SDR ratios, based on cytogenetic models and DNA marker data

Cytogenetic model	FDR	SDR	FDR/SDR
All chromosomes of equal length			
SCO	82.7	34.7	2.4
DCO in chromosomes I, II, and V	81.5	36.8	2.2
Actual chromosome length			
SCO	80.6	36.7	2.2
DCO in chromosomes I, II, and V	80.5	38.2	2.2
Euchromatic regions			
SCO	81.0	36.0	2.2
DCO in chromosomes I, II, and V	79.9	38.2	2.1
DNA/biochemical marker system			
Isozymes (Douches and Quiros 1988)	81.6	39.1	2.2
RAPDs (Vorsa and Rowland 1997)	72.7	—	—
RFLPs (Barone et al. 1995)	71.4	31.8	2.2

SCO, single crossover in each bivalent; DCO, double crossover.

reduced to 75% and increased with SDR to 50%. We considered double crossovers for chromosomes I, II, and V. Because I and II are subtelocentric, both crossovers for chromosomes would most likely be in one arm and have no net effect on transmission of heterozygosity. Chromosome V is the largest metacentric chromosome, so a crossover in each arm would slightly affect transmission if heterozygosity of the total chromosome complement. It roughly reduces FDR transmission by 1.1% and increases SDR transmission by 2.2%.

It is interesting to compare the results obtained by cytogenetic analysis with those from DNA markers. Based on isozyme analysis of 13 loci in potato, Douches and Quiros (1988) found 82% transmission with FDR and 39% with SDR. Vorsa and Rowland (1997) estimated that 72.7% of random amplified polymorphic DNA markers in blueberry 2*n* eggs were heterozygous, indicating that FDR is the predominant mechanism of 2*n* egg formation. However, the clone under study likely produced SDR 2*n* eggs as well. Restriction fragment length polymorphism analysis in potato by Barone et al. (1995) resulted in values of 71% with FDR and 32% with SDR. Although the value of 71% is too low to be explained by cytogenetic events, it is interesting that the FDR/SDR ratio is very similar to the values obtained through cytogenetic analysis and other marker gene results because the distribution of any markers may not be completely random. On this basis, FDR is more than twice as effective in transmitting heterozygosity as SDR.

Table 4. Percent transmission of heterozygosity in gametes of tetrasomic tetraploids and FDR 2*n* gamete/tetrasomic ratios

Model (2 alleles per locus)	Tetrasomic	FDR/tetrasomic
Chromosome segregation	55.5	1.5
10% chromatid segregation	54.8	1.5
50% chromatid segregation	51.6	1.6

It is also important to compare the transmission of heterozygosity in FDR 2*n* gametes with that in *n* gametes of cultivated tetraploid potato because most potato improvement programs emphasize 4*x*-by-4*x* crosses. The transmission of heterozygosity in tetraploid potato with tetrasomic inheritance is about 55% (Table 4). This is based on the assumptions of 2 alleles per locus; simplex, duplex, and triplex genotypes in equal proportions; and chromosome segregation. It is reasonable to assume 2 alleles per locus based on the Douches et al. (1989) isozyme analysis which determined that an average of 2.13 alleles per locus exist in 94 North American potato cultivars. Little information is available on the relative frequency of simplex, duplex, and triplex genotypes, but deviations from equal proportions of the 4 genotypes would not greatly affect results because duplex genotypes transmit 66% of their heterozygosity, and simplex and triplex genotypes both transmit 50%. The occurrence of either chromatid or maximal equational segregation would slightly reduce the amount of heterozygosity transmitted. For example, if 10% of the loci displayed chromatid segregation, the total transmission of heterozygosity would only be reduced from 55% to 54%. At present, we do not have information on the frequency of loci with chromatid segregation.

The important point to be taken from these estimates is that FDR 2*n* gametes from diploids transmit almost 50% more heterozygosity than *n* gametes from the tetraploid potato. These estimates are similar for a wide array of cytogenetic variables, indicating that they are likely to be reasonable predictions of transmission of heterozygosity in other plant species for which cytological data are not available. These estimates provide a rationale for utilizing 2*n* gametes in polyploid crop improvement and a foundation for predicting and interpreting the genetic consequences of 2*n* gametes in their resulting progeny.

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